CESARE F. SACCHI, RENATO SCONFIETTI

Dip.to di Genetica e Microbiologia, Sez. di Ecologia, Università di Pavia
via S. Epifanio, 14 - I 27100 Pavia, Italy

THE RENSCH'S RULE OF SIZES IN LITTORINIDS: AN ECOLOGIST'S POINT OF VIEW

Abstract

An ecological rule – proposed by Rensch for terrestrial Gastropods – states that intraspecific variations in shell size are related to environmental quality. Maximum sizes are attained at environmental optima. Due to their semi-continental way of life as adults, some examples may be looked for in littorinids.

In *Littorina obtusata* (L.) two main size gradients are apparent, one macroclimatic and the other local: from the Channel southward to the Iberian shores, and from sheltered to exposed sites. Shells from Galicia are smaller than from Brittany and Devon. This is probably related to an aerial climate becoming Mediterranean-like southway, while waters conserve North-Atlantic traits.

Local gradients are likely to be the result of biomass reduction and morphological modifications of the sheltering and nourishing patches of the brown seaweeds inhabited by snails. Ecomorphes reflecting kinetic energy variations shall also be considered, as well as a genetic selection expressed by the predominance of morph *olivacea* in calm waters versus *reticulata* in sites fully exposed to waves.

L.mariae Sacchi et Rast. follows parallel biogeographic variations. As for local gradients, however, it behaves in a less schematic way.

Samples of *Melaraphe neritoides* (L.) collected in Naples from breakwaters of a different lithological nature show differences in adult sizes and population densities related more to mechanical structure (substratum unevenness) than to limestone content.

Hydrodynamic and trophic gradients may account for size in confined environments. In the Venice lagoon – the specific topotypic waters – adult specimens of *L.saxatilis* (Olivi) on sheltered, very eutrophicated shores, are twice as large in both sexes than in sites with more stirring waters or lower degrees of trophism.

In insular Indo-pacific *Littoraria* size gradients from sheltered to exposed shores were also observed.

Riassunto

La regola del Rensch nei Littorinidi: punto di vista d'un ecologo

Una regola ecologica, proposta dal Rensch per i Gasteropodi terrestri, afferma che le variazioni intraspecifiche nella mole del guscio sono correlate con la qualità dell'ambiente: le moli massimali si raggiungono in condizioni ambientali ottimali. Qualche esempio se ne potrebbe cercare nei littorinidi, data la loro vita adulta in ambiente semicontinentale.

In *Littorina obtusata* (L.) si notano due principali gradienti di mole: uno macroclimatico, l'altro locale. Dalle coste della Manica, verso sud, fino alle coste iberiche l'uno; da punti riparati a punti battuti dal mare, l'altro.

Le conchiglie della Galizia sono nettamente più piccole che nel Devon ed in Bretagna: conseguenza probabile di un clima aereo che diventa di tipo mediterraneo verso sud, mentre le acque del mare conservano caratteristiche nordatlantiche.

I gradienti locali sono verosimilmente risultato della riduzione di biomassa e delle modificazioni morfologiche nella vegetazione di Feoficee, che offre alle littorine cibo e riparo. Si debbono tenere in conto anche ecomorfosi che riflettono variazioni locali dell'energia cinetica delle onde, accanto ad una selezione genetica tradotta nella predominanza della morfa *olivacea* in acque calme opposta a quella di *reticulata* in greti più battuti dal mare.

L. mariae Sacchi et Rast. segue variazioni biogeografiche parallele a *L. obtusata*, ma per i gradienti locali si comporta in modo meno schematico.

Campioni di *Melaraphe neritoides* (L.) raccolti a Napoli da frangiflutti di differente natura litologica, mostrano differenze nella mole adulta e nella densità di popolazione in relazione piuttosto alla struttura meccanica (rugosità del substrato) che al contenuto di calcio.

Gradienti idrodinamici e trofici possono render conto delle variazioni di mole anche in ambienti confinati. Così in entrambi i sessi gli adulti di *L. saxatilis* (Olivi) dalla laguna di Venezia – località topotipica per questa specie – hanno dimensioni doppie in ambienti protetti, molto eutrofizzati, rispetto agli adulti di greti con acque più mosse, o con minor grado di trofismo.

In *Littoraria* indopacifiche insulari sono stati pure osservati gradienti di mole da tratti riparati a tratti battuti.

Key words: size variations, ecological interpretation, littorinids

Introduction

The ecological rule proposed by RENSCH (1932; 1939) states that in continental Gastropods individuals grow to a larger size where environmental conditions are close to optimality.

Starting from these rather obvious outlines, the ecologist's task consists in identifying, with an acceptable precision, the role of unsuitable factors that interfere with an attainment of large sizes.

Though the rule was advanced for terrestrial snails, maybe a few examples are to be found in littorinids, which as adults show ecological relations allowing some comparisons with terrestrial faunas.

For detailed collecting and analyzing techniques see NATALE and SACCHI (1962), SACCHI (1961, 1966, 1969a), SACCHI and SCONFIETTI (1988, 1992).

Data are filed at the Section of Ecology of the Genetics and Microbiology Department, University of Pavia.

The reason for rejecting the synonymy *Littorina mariae* Sacchi and Rastelli = *Turbo fabalis* Turton are stated in SACCHI (1984).

Latitudinal gradients in *Littorina obtusata* (L.) and L. *mariae* Sacchi et Rastelli

Dissections and measurements – adopting the parameters of COLMAN (1932) – of more than 12000 adult snails (see mainly SACCHI, 1969-a and -b; SACCHI and SCONFIETTI, 1988; 1992) enable us to confirm a general relation, as suggested by FISCHER-PIETTE (1957; 1963) concerning size reduction in intertidal organisms from the Channel shores southward to Galicia, NW Spain. Such a reduction is clearly shown in *L. obtusata* and *L. mariae*. The approximative volume of the shell, calculated by broadly assuming that it forms an ellipsoid with the three axes represented by the Colman's parameters, gives *L. obtusata* from the Galician rìas, in both sexes, a figure slightly more than 40 % as compared with the Roscoff specimens. In *L. mariae* differences are bigger (see Figure 1).

Possibly, a direct role of temperature gradients on the sensitive stages of the organisms, as recently reviewed by ATKINSON (1994) should be considered to explain these macroscopic contrasts, but the climatic features should to be taken into account as a whole. While the sea temperatures are still "northern" in Galicia, the aerial climate becomes mediterranean-like, with a true ombrothermic season of marked aestivation (see Figure 2).

The effects of this contrast (SACCHI, 1964) may be seen in biomass and performance restrictions of the sheltering and feeding vegetation

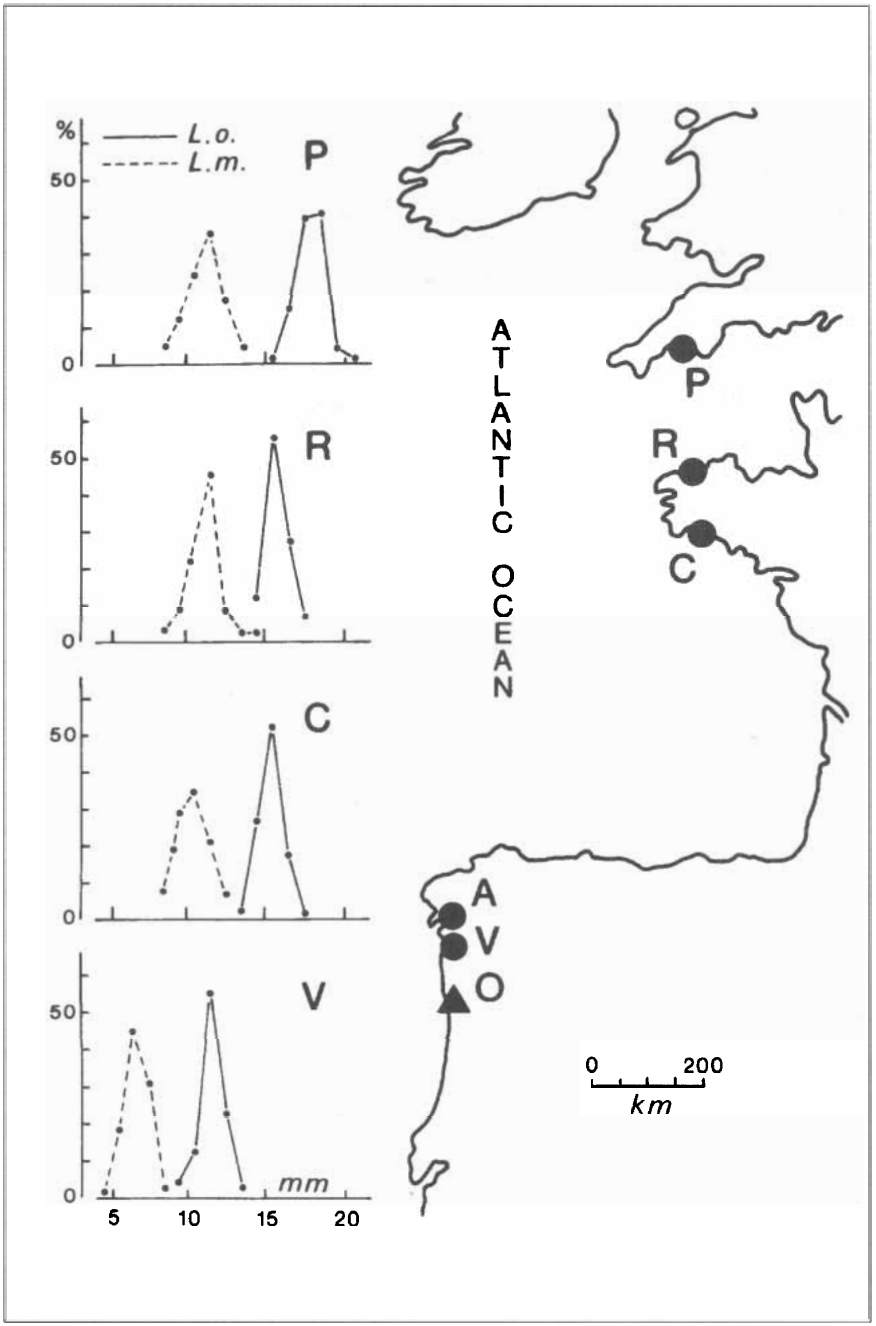

Fig. 1 - Latitudinal variations of the shell parameter "a" (breadth) in *Littorina obtusata* (*L.o.*) and *L. mariae (L.m.).* P = Plymouth: R = Roscoff; C = Concarneau; A = Arosa; V = Vigo; O = Oporto, commonly accepted as the southern limit of the *L. obtusata* group. Redrawn with modifications from SACCHI (1969-c).

of Fucaceae, with a gradual elimination of the components more sensitive to dehydratation – *Ascophyllum nodosum* (L.) and *Fucus serratus* L. – and the restricted activity of the inhabiting snails.

Adult specimens of *L. mariae* from Brittany may be as large, and even larger, than *L. obtusata* from the rìas of Galicia.

As recent experimental work (SANTINI *et al.*, 1995) shows that, in intertidal Gastropods, size reduction within a species would mean reduction in energy costs associated with activity, the above data could be interpreted as being due to a restricted food availability and feeding time, fitting consequently into a selective trophic pattern.

Local size variations in *L. obtusata* and *L. mariae*

A trophic interpretation, as afforded above, could be proposed for local size variations in *L. obtusata*, from sheltered to exposed shores, producing, in the latter, adult shell size reductions up to 35-40 %.

Such gradients were observed in several geographic districts for both sexes. They may be related to restriction in thickness and diversity of the sheltering vegetation of Fucaceae. *Fucus vesiculosus* (L.) a weed typically inhabited and grazed by *L. obtusata*, may be, on rocks very exposed to wave action, only present as its ecomorph *evesiculosus erectus*, granting but a weak support to the snails, as well as a reduced food biomass. *Ascophyllum nodosum* is restricted or absent at such sites.

Hydrodynamic action on the growth rate of snails is also to be taken into account for size gradients of the shells. Genetic components are probably present as the colour morph frequencies vary in calm versus exposed localities. The former show a predominance of morph *olivacea*, the latter of *reticulata*. This gradient was first seen at Roscoff (SACCHI,

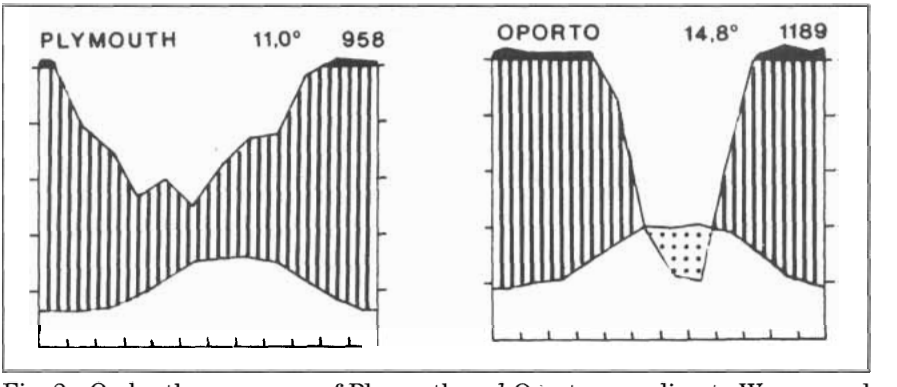

Fig. 2 - Ombrothermograms of Plymouth and Oporto according to WALTER and LIETH (1960-1966). The figures give the annual average temperatures in centigrades and precipitations in millimeters.

1961) then on other Brittany coasts, in Vigo (SACCHI, 1964) and the Plymounth Sound (SACCHI, 1966). In the Rìa de Arosa, however, that is hydrographically far more complicated as the result of several estuaries, both gradients are partially confused (SACCHI, 1984; SACCHI and SCONFIETTI, 1992).

Size gradients may be inverted where "calm" comes to mean excessively stagnant, in very shallow and sheltered waters submitted to marked halo-thermic fluctuations, as found in the so-called "Laguna", in fact a small, closed bay, of the Cies Islands, west of Vigo. Adult snails attain there in both sexes less than 50 % size of individuals living at average-exposed sites in the Rìa, that is 20 % of adult sizes from Roscoff. In a similar site with a poorly energetic supply in Ría de Arosa, slightly larger adults are present. Very small sizes were found even at Plymouth, at semiestuarine sites in the Cattewater (SACCHI, 1966). Possibly such dwarf forms should be ascribed to the "species" *L. aestuarii* (Jeffries) as included in *L. obtusata* by MOYSE *et al.* (1982).

Local gradients are not so linear in *L. mariae*. In exposed rocks at Roscoff relatively large sizes are found. The most exposed east coast, however, shows minimal sizes both in *L. obtusata* and *L. mariae* (SACCHI, 1969-b).

Large sizes in *L. mariae* are actually found in colonies well exposed to waves, provided that the high energy still allow the development of patches of brown seaweeds that play, in this mainly microphagous species, not only a role of shelter but also, though indirectly, of trophic source. Smaller *L. mariae* are found in exposed, but scarcely vegetated boulder beds, as at Pointe Primel. Our data are not in accord with GOODWIN and FISH's (1977) results, who studied a too reduced number of snails to allow comparisons.

Moreover, around Roscoff, a comparison established for littorinid populations from compact rocks, living in high-placed patches of Fucaceae (mainly *Fucus vesiculosus evesiculosus, F. spiralis* and *Pelvetia canaliculata* L.) could not extend to the whole habitat of *L. mariae.* Colonies from the small outcrops of rocks, or isolated stones, among sandy bottoms which are typically covered at a lower intertidal level with patches of *Fucus serratus* L. - a frequent situation elsewhere (WATSON and NORTON, 1987, WILLIAMS, 1990; 1995) - not only show smaller sizes in adult individuals of both sexes, but exhibit other discordant traits.

While the former are characterized by a high frequency of morph *reticulata* with the dark, blackish hues, the latter present, in the Roscoff area, high frequencies of light coloured *reticulata* (SACCHI, 1969-a). Since other differences, e. g. in timing of sexual maturity, may be taken into account too, it is likely to support the hypothesis of an incipient splitting of the two ecological groups of *L.mariae* into separate subspecies (SACCHI, 1969-b). More recent data from REIMCHEN (1981) seem to be in favour of this point of view for Anglesey shores.

Another ecological group of *L.mariae* may be recognized in the Rìa of Arosa. In an extremely sheltered, almost lagoon-like muddy bottom (El Vado) a unique, though very extensive, population was found, living not among brown weeds, but on leaves of Zosteraceae, mainly on *Zostera marina* L. The snails from El Vado are monomorphic *olivacea* (SACCHI, 1984) such monotonous colours making them difficult to discern upon their vegetal substratum even to a human eye, while the particular localization may exclude competition by other littorinids linked to brown weeds. Notwithstanding the very calm site, these uniform green *L. mariae* do not stand out for particular average sizes as compared with other, fucicolous and rock-inhabiting, colonies from Arosa (SACCHI and SCONFIETTI, 1992).

Uncommon conditions for *L.mariae* were also found in the merchant harbour of Brest. As the local aerial climate is sweet and moist, climatic contrasts do not seem important. Mechanical disturbance and chemical pollution are likely to play a role in an extreme dwarfism causing the snails to exhibit adult sizes close to the lowest figures of the Rías (SACCHI, 1968-b). Outside the harbour, on the shores of the Rade de Brest, *L. mariae* attained commonly large sizes (SACCHI, 1968-a).

Variability of gradients in *L. mariae*, when compared with *L. obtusata*, may finally be related to a lesser dependence on a specialized tidal and vegetational level as well as to the more varied ecological opportunities offered by the less stressing mid-tide zones where *L. mariae* frequently settles.

Density, size and substratum in *Melaraphe neritoides* (L.)

According to Rensch, continental snails may attain higher population densities and larger individual sizes when living on soils rich in calcium. It is commonly accepted that on the contrary marine species meet their ionic requirements not from solid substrata but, directly or indirectly, from the water.

From a survey along the shores of Plymouth Sound, that are heterogenous in lithology since Devonian limestone borders on poorly calcareous schists, volcanic rocks and mixed soils, on distribution and size variations of the *L. obtusata* / *L. mariae* group, I concluded (SACCHI, 1967) that "there is no evident relation between the lithological nature of the rocky substratum – calcareous or silicious – and the distribution of either colour morphs or sizes". The snails "seem to be solely affected by exposure to waves and environmental traits ensuing from this".

However it seemed worthwhile to approach the problem in *M. neritoides*, that is in the adult stage, by far the most physiologically "terrestrial" littorinid in the European fauna (NATALE and SACCHI, 1962).

Naples offered a good opportunity for such comparisons, since a row of adjoining breakwaters of different lithological nature rims the city. Three types of rocky substrata were selected, where the snails were followed over a three years period. They were white Apenninian mesozoic limestone; Vesuvian "basalt" (really a very dark coloured tephrite containing an average of 9,4 % CaO) and yellow trachytic tuff (CaO=only 2,5 %).

Contrary to a calcium influence hypothesis, the largest sizes are attained in tuff; second comes the mesozoic limestone. Both on this and tuffs, population densities were markedly higher than on basalt.

Surfaces of basaltic rocks are smoother than both in naturally rugged tuffs and easily abraded limestone. Such mechanical features are likely to offer different chances for settling and staying to littorinids as well as to their accompanying and fostering vegetation. Analogies can be searched in later studies of English Authors (EMSON and FALLER-FRITSCH, 1976; RAFFAELLI and HUGHES, 1978) concerning *M. neritoides* and *L. saxatilis* (Olivi).

To explain densities and size gradients around Naples, the rock colours can be considered more for their thermic capacities in the sunny supralittoral level than as a source of differential post-metamorphosis attraction. Littorinids are known to be capable of discriminating between differences in light intensity (CHARLES, 1966). But around Naples any type of rock, at the wave levels, is uniformly blackish-coloured by a dense belt of endolithic algae.

Variations in confined environments

There is no reason for excluding ecological gradients in littorinids from confined environments where these are heterogeneous. Such is the case of the Lagoon of Venice, the topotype locality of *Littorina saxatilis* (Olivi).

Sharp contrasts in hydrodynamic energy are unlikely to play an important role at Venice, since lagoon waters are typically shallow and smooth everywhere. Venetian *L.saxatillis*, though varied in colour and sculpture, are generally small if compared with Atlantic populations (SACCHI, 1981, SACCHI and TORELLI, 1973, TORELLI, 1984). However, on the SW shores of the island of Poveglia, in one of the most eutrophicated sections of the lagoon (BIRKEMEYER *et al.*, 1998) directly affected by waters from the city, but escaping marine influences, *L.saxatilis* attains average adult sizes (mm 11,1-12,7 height x 10,6-11,2 breadth) that are twice as large as the sizes found in peripheral suburban canals (mm 6,6-7,5 x 5,6-6,5: data in preparation).

One can also examine environments confined not by mainland, but by sea, i.e.islands. Size gradients occur in islands as along mainland shores, where comparable factors may be expected to work (SACCHI, 1994).

Fig. 3 shows specimens from the Réunion, southern Indian Ocean. Parallel variations are seen in two syntopic *Littoraria, L.glabrata* (Philippi) and *L.mauritiana* (Lamarck); samples from an exposed cape north of Saint Leu (western coast) are smaller than shells from a small estuary close to town (see Figure 3).

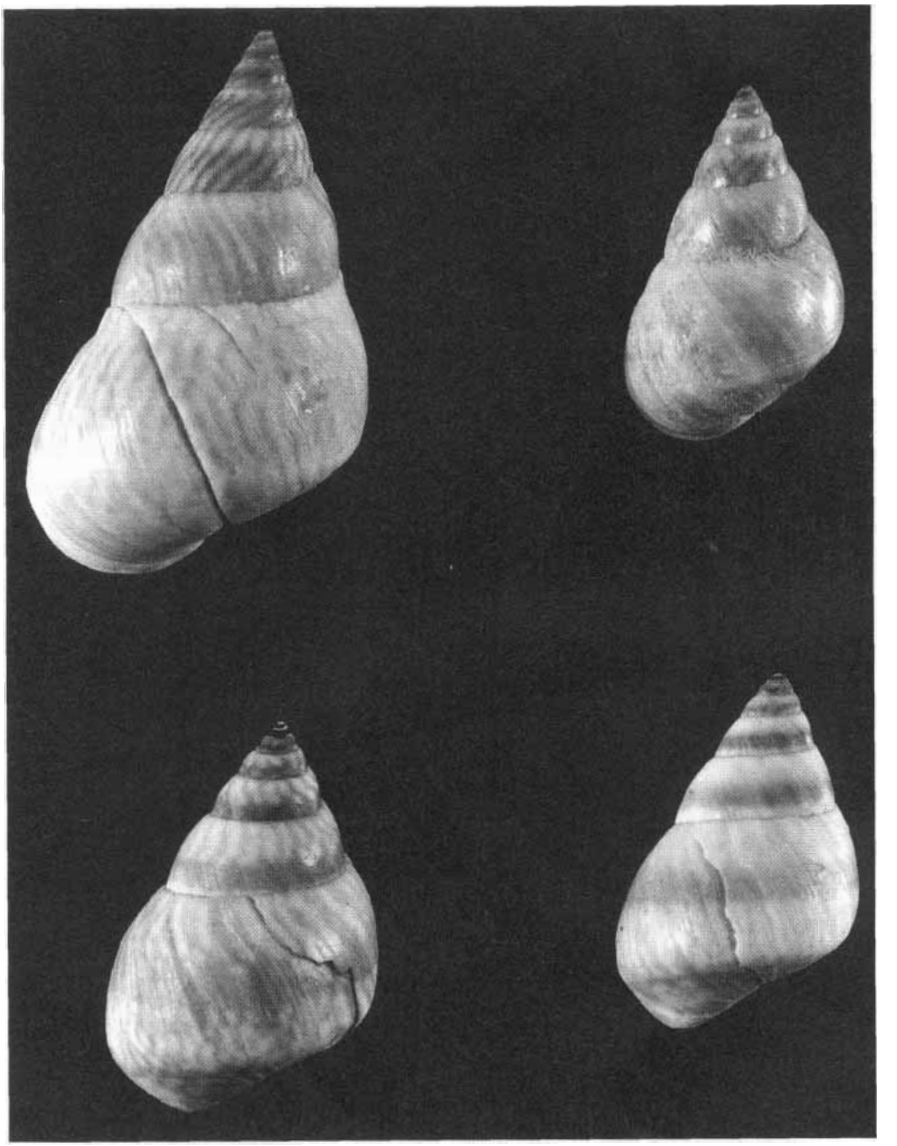

Fig. 3 - Parallel size variations in two *Littoraria* species of Saint Leu, island of Réunion. Above, *L. glabrata* (Philippi); below, *L. mauritiana* (Lam.). Right, from an exposed cape; left, from an estuary. All are female shells. The biggest *L. glabrata* is 21 mm high (October 1994).

Conclusions

Ecological rules are, in my opinion, statistical ensembles defined less to codify in a holistic perspective static data, than to guide ecological and evolutionary researches along reductionistic rails for interpreting the various, dynamic realities of the field biology.

In this sense, some aspects of the Rensch's rule of sizes may be cautiously accepted for littorinids.

We are on the threshold of problems the solution to which would enable us to stress gradients with a realistic evolutionary meaning at geographic and ecological levels, as presented in the first quarter of our century by the evolutionary ecologist Paul PELSENEER (1920).

More data are needed from field and experimental studies. Contributions from geneticists and demographers are necessary. To obtain acceptable results it would be fundamental to take into account not only microsystematic and biometric data, but several additional aspects, as biological rhythms, migrations, short-term selective processes as studied by SEELEY (1986).

In this context the ecologist's work may be viewed as a modest one. Yet naturalists, as VERMEJI (1994) points out, are expected to have their appropriate function in these most interesting essays of the modern evolutionary biology.

Thanks are due to the referees who improved the text of this article, presented by Sacchi at the Fifth International Symposium of Littorinid Biology (Cork, 7-12 September 1996).

REFERENCES

ATKINSON D., 1994 – Temperature and organism size. A biological law for ectotherms? *Adv. Ecol. Research* 25, pp. 1-58.

BIRKEMEYER T., OCCHIPINTI A., SACCHI C.F. 1998 – Indicatori ambientali in Laguna di Venezia: Proposta di una classificazione basata sulle comunità sessili. *Boll. mus. civ. St. nat.* Venezia 48, pp. 267-276.

CHARLES G.M., 1966 – Sense organs (less Cephalopods). In Wilbur, K.M. and Yonge, C.M. (Eds). *Physiology of Mollusca*, Academic Press, New York and London, 2, pp. 455-521.

COLMAN J.H. (1932) A statistical analysis of the species concept in *Littorina*. *Biol. Bull.* 62, pp. 223-243.

EMSON R.H., FALLER-FRITSCH R. J., 1976 – An experimental investigation into the effect of crevice availability on abundance and size-structure in a population of *Littorina rudis*. *J. exper. mar. Biol. Ecol.* 23, pp. 285-297.

FISCHER-PIETTE E., 1957 – Sur des déplacements de frontières biogéographiques observés le long des côtes ibériques dans le domaine intercotidal. *Publ. Inst. Biol. apl. Barcelona* 26, pp. 35-40.

FISCHER-PIETTE E., 1963 – La distribution des principaux organismes intercotidaux nord-ibériques en 1954-1955. *Ann. Inst. Océan.* 40, pp. 165-310.

GOODWIN B.I., FISH J.D., 1977 – Inter- and intra-specific variation in *Littorina obtusata* and *L. mariae*. *J. Moll. Stud.* 43, pp. 241-254.

MOYSE J., THORPE J.P., AL HAMADABI E., 1982 – The status of *Littorina aestuarii* Jeffrey: an approach using morphology and biochemical genetics. *J. Conch. London* 31, pp. 7-15.

NATALE T., SACCHI C.F., 1962 – Sur les relations entre le chimisme du substratum, la densité des peuplements et la taille chez *Littorina neritoides* (L.) de la baie de Naples. *Pubbl. Staz. zool. Napoli* 32 suppl., pp. 133-144.

PELSENEER P., 1920 – Les variations et leur hérédité chez les Mollusques. *Mém. Acad. Royale Belgique Cl. Sciences* (2) 5, 5-826.

RAFFAELLI D.G., HUGHES R.N., 1978 – The effect of crevice size and availability on populations of *Littorina rudis* and *L. neritoides*. *J. anim. Ecol.* 47, pp. 7-83.

REIMCHEN T. E., 1981 – Microgeographical variation in *Littorina mariae* Sacchi et Rastelli and a taxonomic consideration. *J. Conch. London* 30, pp. 341-350.

RENSCH B., 1932 – Ueber die Abhängigkeit des Grosse, relativen Gewichte und der Oberflächenstruktur des Landschneckenschalen von den Umweltsfaktoren. *Z. Morph. Oekol. Tiere* 25, pp. 757-807.

RENSCH B., 1939 – Klimatische Auslese von Grösservarianter. *Arch. Naturg.* N. F. 8, pp. 89-129.

SACCHI C. F., 1961 – Contribution à l'étude des rapport écologie / polychromatisme chez un Prosobranche intercotidal, *Littorina obtusata* (L.) à Roscoff. *Cah. Biol. mar.* 2, pp. 271-290.

SACCHI C. F., 1964 – Relazioni tra ecologia e polimorfismo nel Prosobranco intercotidale *Littorina obtusata* (L.) IV - Studio sulla rìa di Vigo. *Arch. zool. it.* 49, 93-156.

SACCHI C.F., 1966 – Contribution à l'étude des rapports entre variabilité et écologie chez un Prosobranche intertidal, *Littorina obtusata* (L.) V- Recherches dans le Plymouth Sound (Angleterre SW). *Cah. Biol. mar.* 7, pp. 281-294.

SACCHI C. F., 1967 – Variabilità ed ambiente nella coppia di specie intertidali *Littorina obtusata* (L.) e *L. mariae* Sacchi et Rastelli (Gastropoda, Prosobranchia) a Concarneau (Bretagna meridionale). *Studia Ghisleriana* (3) 2, pp. 339-355.

SACCHI C. F. – 1968-a – Sur le dimorphisme sexuel de *Littorina mariae* (Gastropoda, Prosobranchia). *C. R. Acad. Sc. Paris* 266, pp. 2483-2485.

SACCHI C. F., 1968-b – Une population exceptionnelle de *Littorina mariae* (Gastropoda, Prosobranchia) à Brest (Nord-Finistère). *Natura, Milano* 59, pp. 213-219.

SACCHI C. F., 1969-a – Recherches sur l'écologie comparée de *Littorina obtusata* (L.) et de *L. mariae* Sacchi et Rast. en Galice et en Bretagne. *Investigaciòn pesquera* 33, pp. 381-414.

SACCHI C.F., 1969-b – Ricerche biometriche sul dimorfismo sessuale della coppia di specie intertidali *Littorina obtusata* (L.) et *L. mariae* Sacchi et Rast. in Bretagna ed in Galizia. *Boll. Pesca, Piscic. Idrobiol.* 24, pp. 33-47.

SACCHI C.F., 1969-c – Considérations écologiques sur les peuplements de marée: aspects généraux et problèmes méditerranéens. *Pubbl. Staz. zool. Napoli* 37 suppl., pp. 73-123.

SACCHI C.F., 1981 – Ricerche sulle variazioni di mole in *Littorina saxatilis* (Olivi) e sul loro significato ecologico. *Boll. Mus. civ. St. nat. Venezia* 31, pp. 51-67.

SACCHI C.F., 1984 – Recherches sur l'écologie comparée de *L. obtusata* (L.) et de *L. mariae* Sacchi et Rast. dans la Ria de Arosa, Espagne nord-occidentale. I - Caractères des peuplements, polychromatisme, rapport des sexes. *Atti Soc. it. Sc. nat.* 125, pp. 209-232.

SACCHI C. F., 1994 – Contribution à l'étude de deux *Littoraria* des îles sud-pacifiques. *Boll. malacologico* 30, 49-66.

SACCHI C. F., SCONFIETTI R., 1988 – Recherches sur l'écologie comparée de *Littorina obtusata* (L.) et de *L. mariae* Sacchi et Rast. dans la Ria de Arosa, Espagne nord-occidentale. III -Dimorphisme sexuel et gradients de taille en *L. obtusata*. *Atti Soc. it. Sc. nat.* 129, pp. 285-304.

SACCHI C.F., SCONFIETTI R., 1992 – Id. id. IV - Dimorphisme sexuel et gradients de taille en *Littorina mariae*. *Atti Soc. it. Sc. nat.* 132, pp. 105-118.

SACCHI C.F., TORELLI A.M., 1973 – Présence, variabilité et cycle biotique de *Littorina saxatilis* (Olivi) dans la lagune de Venise. *Atti Soc. Peloritana di Sc.* 19, pp. 181-188.

SANTINI G., CHELAZZI G., DELLA SANTINA P., 1995 – Size-related functional and energetics constraints in the foraging of the limpet *Patella vulgata* (Mollusca, Gastropoda). *Functional Ecology* 9, pp. 551-558.

SEELEY R.H., 1986 – Intense natural selection caused a rapid morphological transition in a living marine snail. *Proc. nat. Acad. USA* 83, pp. 6897-6901.

TORELLI A., 1984 – *Littorina saxatilis* (Olivi) nella laguna di Venezia: sue variazioni e ciclo biologico in relazione all'ambiente. *Atti Soc. it. Sc. nat.* 125, pp. 112-120.

VERMEIJ G. J., 1994 – The evolutionary interaction among species: selection, escalation and coevolution. *Ann. Rev. Ecol. Syst.* 25, pp. 219-236.

WALTER R., LIETH H., 1960-1966 – Klimadiagramm Weltatlas. G. Fischer, Iena. *Westeuropa, II (2) 1,4; Iberischen Halbinsel (3) 1,2.*

WATSON D.C., NORTON T.A., 1987 – The habitat and feeding preferences of *Littorina obtusata* (L.) and *L. mariae* Sacchi and Rastelli. *J. exper. mar. Biol. Ecol.* 112, pp. 61-72.

WILLIAMS G.A., 1990 – The comparative ecology of the flat periwinkles, *Littorina obtusata* (L.) and *L. mariae* Sacchi and Rastelli. *Field Studies* 7, pp. 469-482.

WILLIAMS G. A., 1995 – Maintenance of zonation patterns in two species of flat periwinkle *Littorina obtusata* and *L. mariae. Hydrobiologia* 309, pp. 143-150.